ZooKeys 472: 1–25 (2015)
doi: 10.3897/zookeys.472.8547
http://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

Southern hemisphere deep-water stylasterid corals including a new species, *Errina labrosa* sp. n. (Cnidaria, Hydrozoa, Stylasteridae), with notes on some symbiotic scalpellids (Cirripedia, Thoracica, Scalpellidae)

Daniela Pica[1], Stephen D. Cairns[2], Stefania Puce[1], William A. Newman[3]

1 *Department of Life and Environmental Sciences, Polytechnic University of Marche, Via Brecce Bianche, 60131 Ancona, Italy* **2** *Department of Invertebrate Zoology, Smithsonian Institution, Washington, D.C., 20560, U.S.A.* **3** *Scripps Institution of Oceanography, La Jolla, California 92093-0202, U.S.A.*

Corresponding author: *Daniela Pica* (daniela.pica@gmail.com)

Academic editor: *B.W. Hoeksema* | Received 3 September 2014 | Accepted 8 December 2014 | Published 19 January 2015

http://zoobank.org/5320D702-4D0E-490D-8E16-C6A98102E6FC

Citation: Pica D, Cairns SD, Puce S, Newman WA (2015) Southern hemisphere deep-water stylasterid corals including a new species, *Errina labrosa* sp. n. (Cnidaria, Hydrozoa, Stylasteridae), with notes on some symbiotic scalpellids (Cirripedia, Thoracica, Scalpellidae). ZooKeys 472: 1–25. doi: 10.3897/zookeys.472.8547

Abstract

A number of stylasterid corals are known to act as host species and create refuges for a variety of mobile and sessile organisms, which enhances their habitat complexity. These include annelids, anthozoans, cirripeds, copepods, cyanobacteria, echinoderms, gastropods, hydroids and sponges. Here we report the first evidence of a diverse association between stylasterids and scalpellid pedunculate barnacles and describe a new stylasterid species, *Errina labrosa*, from the Tristan da Cunha Archipelago. Overall, five stylasterid species are found to host eight scalpellid barnacles from several biogeographic regions in the southern hemisphere (Southern Ocean, temperate South America and the southern Indo-Pacific realms). There is an apparent lack of specificity in this kind of association and different grades of reaction to the symbiosis have been observed in the coral. These records suggest that the association between pedunculate barnacles and hard stylasterid corals has a wide distribution among different biogeographic realms and that it is relatively rare and confined largely to deep water.

Keywords

Deep-water symbiosis, Scalpellidae, Stylasteridae, new species

Copyright *Daniela Pica et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Many stylasterid corals, like their shallow-water largely scleractinian counterparts (see e.g. Patton 1994, Stella et al. 2011, Hoeksema et al. 2012), are considered habitat-forming species because they contribute to the structuring of deep and shallow water coral banks (Roberts et al. 2006, Häussermann and Försterra 2007). In this context the tridimensional structure of their calcareous skeleton should enhance the complexity of the habitat, by creating refuges for a variety of mobile and sessile organisms (Braga-Henriques et al. 2010): basibionts for many other invertebrate such as annelids, anthozoans, cirripeds, copepods, cyanobacteria, echinoderms, gastropods, hydroids and sponges (Zibrowius 1981, Braga-Henriques et al. 2010, Goud and Hoeksema 2001, Pica et al. 2012, Puce et al. 2009). Species of the gastropod *Pedicularia*, considered obligate symbionts of Stylasteridae, usually assume the colour of the host colony and modify the branch coral surface where they reside (Zibrowius 1981, Goud and Hoeksema 2001, Cairns and Zibrowius 2013). Other organisms induce changes in the coral morphology and growth, like copepods that induce the formation of a gall on the coral branches (Zibrowius 1981, Buhl-Mortensen and Mortensen 2004a) and balanomorph or acorn barnacles (Zibrowius 1981) that usually are completely covered by the coral coenosteum. The presence of polychaetes on stylasterid colonies seems to occur in about 30% of the stylasterid species and frequently induces pronounced changes in the growth form and branching pattern in many species. For example, in *Inferiolabiata labiata* (Moseley, 1879) the polynoid *Polyeunoa laevis* McIntosh, 1885 induces modifications in the growing branches prior to the production of a reticulate tube in which the worm travels (Moseley 1879, Cairns 1983a). Those epibionts probably receive protection from predators, and also access to food is increased due to the tridimensional shape of the colonies (Braga-Henriques et al. 2010).

Such associations between cnidarians and other invertebrates are fairly common. Crustaceans, in particular cirripeds, are most prevalent in shallow water, the latter largely with corals having calcareous skeletons. The most notable include the burrowing barnacles or acrothoracicans (Kolbasov 2009) and thoracican coral barnacles generally belonging to the sessile balanomorph family Pyrgomatidae (Ross and Newman 1973). Such obligate, often host specific forms attain a remarkable diversity on scleractinian corals (Newman et al. 1976, Malay and Michonneau 2014), especially regarding shell modifications in species that have become nutritionally parasitic (Ross and Newman 1995).

The general situation in deep water is quite different as it is pedunculate scalpellomorphs rather than sessile balanomorphs that predominate (Newman and Ross 1971, cf. lepadomorph/balanomorph ratio). In their review of deep-water coral symbiosis, Buhl-Mortensen and Mortensen (2004b) reported on 74 host species (33 gorgonians, 29 scleractinians, seven alcyonaceans, and five antipatharians, but no stylasterids) with obligate as well as facultative associates. They conclude that Cirripedia (including their close relatives, the Ascothoracida), are the most common crustacean taxa associates of

deep-water corals. While the ascothoracids range from somewhat vagile ectoparasites to highly modified gall-forming endoparasites, the scalpellomorph pedunculates have made no obvious morphological adaptations to their hosts. However, it has been shown that calices of deep-water scleractinians such as *Lophelia pertusa* (Linnaeus, 1758), can grow up around a substantial portion of the peduncle of the scalpellomorphs (Newman et al. 2002), and herein we demonstrate for the first time that the coenosteum of stylasterid corals can do likewise. Furthermore, this paper reports the first evidence of a diverse association between stylasterids and scalpellid pedunculate barnacles from several southern biogeographic regions and describes a new stylasterid species from the Tristan da Cunha Archipelago involved in this symbiosis.

Methods

The Stylasteridae collections of several European Museums have been studied: MNA – Museo Nazionale dell'Antartide "Felice Ippolito", Italy; Museo di Storia Naturale of Genova, Italy; BNHM – Natural History Museum of London, United Kingdom; MNHN – Muséum National d'Histoire Naturelle of Paris, France; RMNH and ZMA in Naturalis Biodiversity Center of Leiden, Nederland. A number of specimens with pedunculate barnacles on them were examined for further analyses. The coral specimens (dry or preserved in ethanol) were, largely from the South Atlantic Ocean and the Antarctic and Sub-Antarctic region, whereas *Stephanohelia* corals were from off New Caledonia (South Pacific). The morphology of the specimens and details of the associations were first examined using a stereomicroscope. Selected portions were prepared for the scanning electron microscope (SEM) and photographic analyses. Longitudinal sections of coral branches were cut with an electric grinder in order to study the internal structures. Small portions of the coral were treated with sodium hypochlorite for 10 minutes, rinsed with distilled water, and dried, and coated with gold–palladium in a Balzer Union evaporator and examined with a Philips XL20 SEM.

Results

Among a total of about 600 stylasterid colonies observed, only 11 (<2%) belonging to five species revealed the presence of scalpellid barnacles (Table 1). The range of morphological responses of the corals to a notable diversity of barnacles was initially not fully appreciated owing to the scarcity of the material. The identification of the barnacles has been limited to illustrated specimens and while at least two subfamilies of the species-rich Scalpellidae are represented, it was not possible to identify all to species or even genus level. Nonetheless, this paper sheds considerable light on this kind of interspecific relationship and sets the stage for future taxonomic work on the barnacles involved.

Systematic part

Phylum Cnidaria
Class Hydrozoa Owen, 1843
Subclass Hydroidolina Collins & Marques, 2004
Order Anthoathecata Cornelius, 1992
Suborder Filifera Kühn, 1913
Family Stylasteridae Gray, 1847

Genus *Stephanohelia* Cairns, 1991

Diagnosis. Colonies with irregular shape, all with commensal polychaetes. Branches polychotomous with gastropores exclusively in the branch axils. Coenosteal texture linear-imbricate. Gastrostyle massive. Dactylopore spines small and without dactylostyles. Male ampullae superficial.

Discussion. The genus *Stephanohelia* is monospecific (Cairns 1991). The genus is easily diagnosed by its characteristic polychotomous branching and the gastropores exclusively at branch axils.

Type species. *Stephanohelia praecipua* Cairns, 1991.

Depth range. 318–793 m.

Distribution. New Zealand and New Caledonia.

Stephanohelia sp.

Figure 1

Material studied. Three colonies of sample MNHN IK 2010-152: expedition MUSORSTOM 4 N/O Vauban, Sta. CP194, 18°53' S, 163°22' E, New Caledonia, 550 m depth 19 September 1985 (in ethanol).

Description. Coral colonies arborescent, up to 8 cm long and 7 cm wide, with the basal branches up to 1.5 cm in diameter (Figure 1a). They are characterised by few main branches that are uniplanar around which several polychotomously tiny branches originate, formed by two to five branchlets (Figure 1b). The tiny branches are characterised by small abcauline spines (Figures 1b, c), up to 20 μm tall, mainly on the lateral edges. The branches are oval in cross-section. The tiny branches on both faces of the main branches are often anastomose, forming a gallery, which is caused by a commensal polychaete (Figure 1a). The colonies are attached to the substrate by an incrusting base. The colour of the coenosteum is white (Figure 1a). The coenosteal texture is linear-imbricate, composed of platelets irregular in shape and showing an alternating polarity (Figure 1d). The coenosteum is pierced by numerous coenosteal pores, 15-22-30 μm in diameter (Figure 1d). The strips are not well defined. The coenosteum is white.

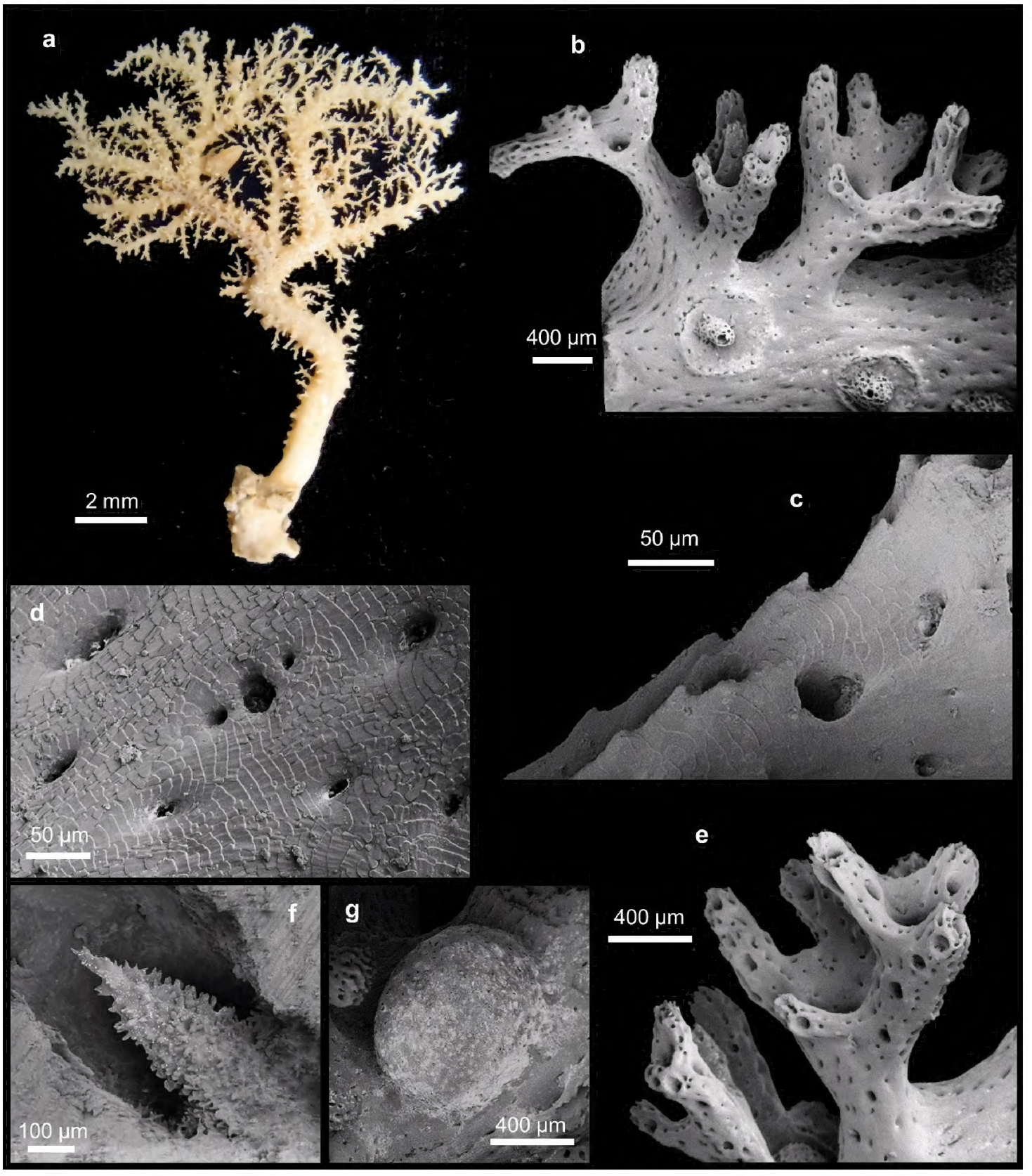

Figure 1. *Stephanohelia* sp. **a** Colony. SEM micrographs of **b** branch with polychotomous tiny branches and male ampullae **c** small abcauline spines **d** texture **e** polychotomous branches with aligned dactylopores **f** gastrostyle **g** female ampulla.

Gastropores are circular, 100-175-230 µm in diameter, occurring exclusively at branching axils (Figure 1e). The gastropore tubes are cylindrical to conical in apical branches where they are less deep. The gastrostyle tips are visible on the coenosteum surface. The gastrostyles are robust and tree-like in shape without ridges and ornamented with multi-tipped spines (Figure 1f). The gastrostyles measure 96-170-205 µm in length and 50-80-100 µm in diameter (L:D=1.8–2.6). A ring palisade is not present.

The dactylopores are flush with coenosteum and aligned on branch edges (Figure 1e). They are circular in shape and 40-60-95 μm in diameter. Dactylostyles are absent.

The female ampullae are round, superficial, 600-820-900 μm in diameter, and have a smooth surface (Figure 1g). They are distributed uniformly around the branches. Male ampullae are 400-510-600 μm in diameter and characterised by a round depression with a small central dome (Figure 1b). The domes vary in shape and have a highly perforate surface, usually with an apical pore (Figure 1b).

Remarks. The characteristic shape of the colonies with polychotomous branching, the presence of the gastropores exclusively at branch axils, the large gastrostyles and the absence of the ring palisade and the dactylostyles are characteristic for *Stephanohelia*. This species differs from the type species, *S. praecipua*, mainly in the gastrostyle shape. In fact, *S. praecipua* has a gastrostyle characterised by a main basal shaft with a very expanded midsection and a slender tip. The scarcity of the analysed material is insufficient to enable the description of a new species.

Genus *Inferiolabiata* Broch, 1951

Diagnosis. Colonies commonly associated with a commensal polychaete. Gastropores and dactylopores randomly distributed. Coenosteal texture linear- or reticulate-imbricate. Gastrostyles are present but a ring palisade is usually absent. Tabulae often present. Dactylopore spines with a primarily abcauline dactylotome. Dactylostyles present. Ampullae superficial.

Discussion. The genus *Inferiolabiata* includes four species (Cairns and Zibrowius 2013). The present material represents part of the first record of identified stylasterid corals from the Tristan da Cunha Archipelago.

Type species. *Errina labiata* Moseley, 1879.

Depth range. 80–2100 m.

Distribution. Tristan da Cunha Archipelago, South Africa, Antarctica and Sub-Antarctic area, New Zealand.

Inferiolabiata spinosa Cairns, 1991

Inferiolabiata spinosa Cairns 1991: 42; Cairns and Zibrowius 2013: 14.

Material studied. BNHM 1977.8.10.2: two broken colonies and seven fragments, *Discovery* Expedition Sta. 6, Tristan da Cunha, 3 miles N 30° E of Settlement, 80–140 m depth, 1 February 1926 (in ethanol).

Remarks. The genus *Inferiolabiata* consists of only four species: *I. labiata* (Moseley, 1879), *I. lowei* (Cairns, 1983a), *I. spinosa* Cairns, 1991 and *I. africana* Cairns & Zibrowius, 2013. Our specimens match *I. spinosa* described from New Zealand and South Africa (Cairns 1991, Cairns and Zibrowius 2013). They only differ in having

longer and thinner gastrostyles (L:D up to 15), in lacking a well-defined ring palisade, and the presence of two unlinear series of dactylostyles instead of three.

This is the first record of *I. spinosa* from the Atlantic and together with *Errina labrosa* sp. n. (see below), it is part of the only known stylasterid fauna reported from Tristan da Cunha Archipelago.

Genus *Errina* Gray, 1835

Diagnosis. Gastropores and dactylopores randomly distributed. Coenosteal texture reticulate-granular and linear-imbricate. Lower gastropore lip present in some specimens. Gastrostyles present but ring palisade usually absent. Dactylopore spines represented by up to two types and varying in shape and dimension. Dactylopore spines with a primarily adcauline dactylotome. Dactylostyles rarely present. Ampullae superficial and deep.

Discussion. The genus *Errina* includes 25 Recent species and one extinct species (Cairns 2014). The presence of dactylostyles in this genus is reported here for the first time.

Type species. *Millepora aspera* Linnaeus, 1767.

Depth range. 6–1772 m.

Distribution. North Atlantic, Mediterranean Sea, Galápagos, South Africa, Antarctica and Sub-Antarctic area, New Zealand, Japan and Tristan da Cunha Archipelago.

Errina antarctica (Gray, 1872)

See Cairns (1983a: 83) for synonymy.

Material studied. BNHM 1977.8.10.20: two colonies, *Discovery* Expedition, Sta. WS 248, Falkland Islands 52°40'00"S 58°30'00"W, 210-242 m depth, 20 July 1928, (preserved in ethanol); BNHM 1977.8.10.17: five broken colonies, *Discovery* Expedition, Sta. WS 841, 54°11'S 60°23"W, 200-370 m depth, 6 February 1932 (preserved in ethanol); BNHM 1977.8.10.34: 3 broken colonies and fragments, *Discovery* Expedition, Sta. WS 85, Falkland Islands, 52°09'00"S 54°14'00"W, 79 m depth, 25 March 1927 (dry).

Remarks. Within the genus *Errina* our specimens match *Errina antarctica* as described by Cairns (1983a) in all aspects of the colony morphology (see remarks of *E. fissurata*).

Errina fissurata (Gray, 1872)

Figure 2

Madrepora fissurata Stokes 1847: 336
Errina fissurata Gray 1872: 745; Moseley 1879: 479; 1881: 84; Boschma 1957: 53; 1964: 284; Boschma and Lowe 1969: 15; Cairns 1983a: 89.
Labiopora fissurata Hickson 1912: 878.

Errina (*Eu-Errina*) *fissurata* Broch 1942: 38.
Errina (*Eu-Errina*) *antarctica* Broch 1951: 35 (part of material from sta. 1948).
Errina (*Errina*) *fissurata* Boschma 1963: 337; Cairns 1983a: 89.
Errina antarctica Boschma 1966: 109 (part of material from sta. 30).

Material studied. MNA 3070, MNA 3071: two colonies, Cruise Carbonant 2002, Sta. 24, 72°30'456"S, 174°05'552"E, 438 m depth, 13 January 2002 (in ethanol); MNA 3079, MNA 3080, MNA 3081, MNA 3082, MNA 3086: a total of five colonies, Cruise Tangaroa 2004, Sta. 77, 72°07'47"S, 172°42'36"E, 499 m depth, 14 February 2004 (dry); BNHM 1977.8.10.26: one colony, *Discovery* Expedition, Sta. 1948, 60°49'24"S, 52°40'00"W,490–610 m depth, 4 January 1937 (in ethanol).

Description. Specimens consist of up to 16.4 cm long broken branches of uniplanar colonies, all lacking the base (Figure 2a). The branching pattern is irregular and dichotomous, most branches oriented nearly parallel (Figure 2a). They are oval in cross-section and up to 6 mm in diameter. The blunt tips are 2–3 mm in diameter (Figure 2b).

The colour of the coenosteum is pale orange (Figure 2a) with the core of the branches white. The texture is reticulate-granular with small and rounded granules 1.4–10 μm in diameter (Figures 2c, d). On the surface there are non-linear slits, up to 140 μm wide and provided with teeth projecting inward (Figure 2d). They connect the coenosteal pores, 20–30 μm in diameter (Figure 2d).

The gastropores and dactylopores are scattered over the coenosteum (Figure 2b). They are decreasing in abundance and density from the tip of each branch towards the base, being mainly present on the lateral branch edges and almost absent on the faces while they are generally lacking in the basal region. The round gastropores, 100–300 μm in diameter, are not lipped and the gastrostyle tips are visible from the coenosteum surface (Figure 2b). The gastrostyles are robust and lanceolate without ridges and have multi-tipped bifurcating spines (Figures 2e, f). They are up to 470 μm long and up to 220 μm in diameter (L:D=1.7–2.9). Ring palisades and tabulae are not recorded (Figure 2e).

The coenosteum surface contains two kinds of dactylopores, with either large or small spines, which protrude perpendicularly from it (Figure 2g). The large spines are U-shaped in cross-section and have an adcauline opening; they are mainly present in the distal portion of the branches (Figures 2h–j). They are 250–400 μm long with a diameter of 250–500 μm and are characterised by a thick porous wall (Figure 2h). Laterally they are composed of smooth overlapping platelets, while the internal wall is characterised by the typical reticulate texture (Figures 2i, j). The dactylotome is 60–110 μm wide (Figure 2j). From the apex to the base, the large dactylopore spines tend to become flush with the coenosteum and to disappear from the colony faces, remaining only on the lateral branch edges. The small spines are scattered between the large ones (Figures 2g, h, k), and, toward the base of the colony they become increasingly difficult to distinguish from the large dactylopores. Their external wall is smooth or reticulate and measures 60–140 × 60–85 μm in diameter and up to 70 μm in length (Figures 2h, k). The dactylotome is randomly

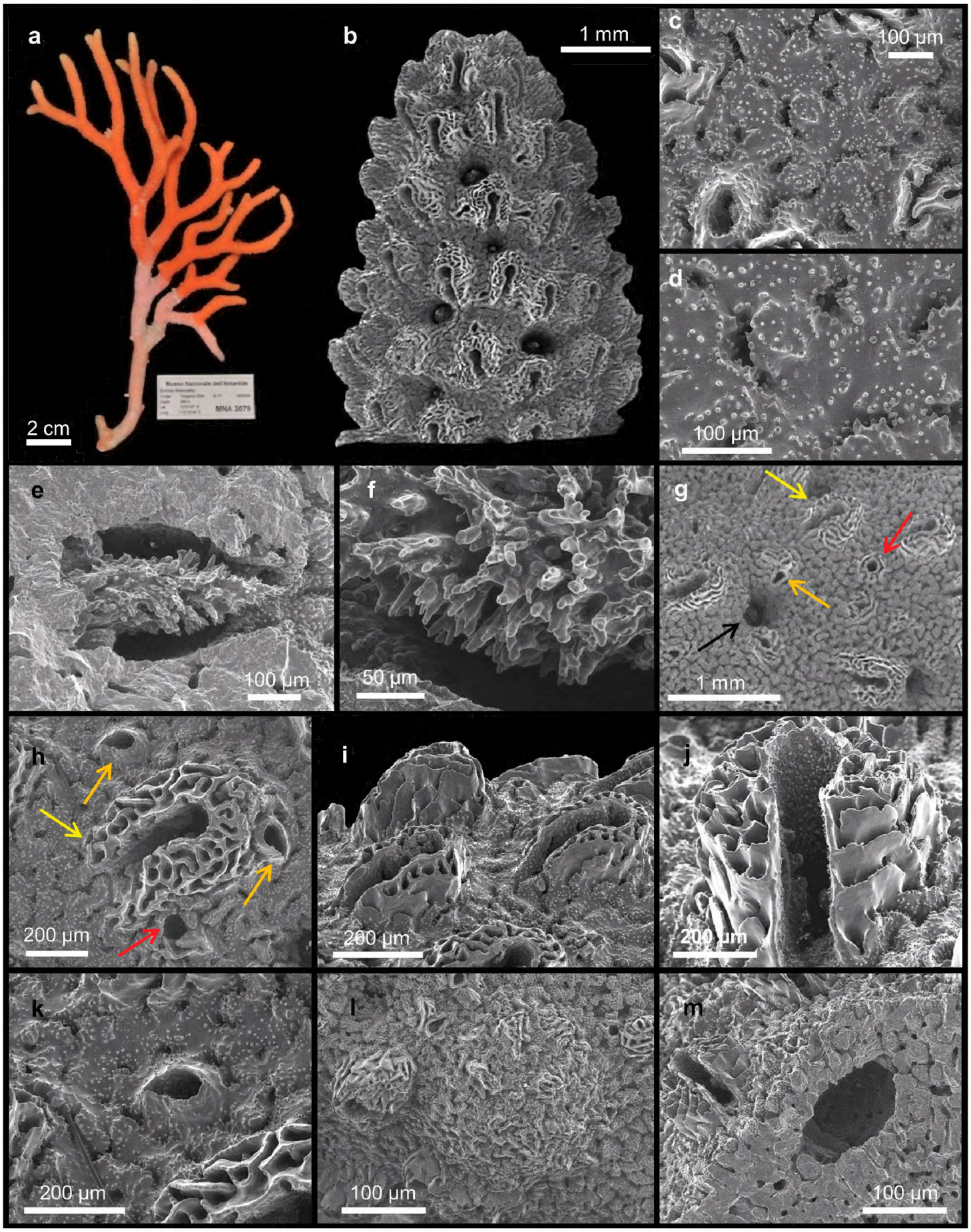

Figure 2. *Errina fissurata* Gray, 1872. **a** Colony. SEM micrographs of **b** apical branch **c–d** reticulate-granular coenosteal texture **e** gastrostyle **f** bifurcating spines of gastrostyle **g** different type of pores: gastropore (black arrow), large dactylopore spine (yellow arrow), small dactylopore spine (orange arrow) and large round pore (red arrow) **h** large dactylopore spine (yellow arrow), small dactylopore spines (orange arrows) and large round pore (red arrow) **i** large adcauline dactylopore spines **j** dactylostyles **k** small dactylopore spine **l** female ampulla **m** male ampulla.

oriented (Figure 2h). Dactylostyles are present only in the large spines (Figure 2j). They are composed by rudimentary elements up to 35 μm long and are arranged in two linear series on the lateral internal wall of the spine.

Large round pores (50–90 μm in diameter) almost flush with the coenosteum. They are scattered over the coral surface between the dactylopore spines (Figures 2g, h).

The colonies present sexual dimorphism in both size and position of the ampullae. The female colonies have round ampullae (up to 1 mm in diameter) that protrude from the coenosteum surface (Figure 2l). Small dactylopores are frequently present over the ampullae. The efferent pores are up to 175 μm in diameter and may be visible laterally. Male colonies have smaller, round to elliptical ampullae (up to 500 μm in diameter), which are partially embedded in the coenosteum and almost no detectable at the surface (Figure 2m).

Remarks. In the Antarctic and Sub-Antarctic region 11 *Errina* species have been recorded (Cairns 1983b, 1991). Among them, *E. fissurata* and *E. antarctica* are very similar to our specimens in various characters such as coenosteum colour and texture, non-lipped gastropore, and in having two kinds of dactylopores. The characteristic shape of the large dactylopore spines, the shape of the gastrostyles and the dimorphism of the ampullae reported in *E. fissurata* clearly match with our Antarctic specimens. Moreover, *E. fissurata* and *E. antarctica* show a distinct geographical and bathymetric distribution: *E. fissurata* is described around continental Antarctic, and almost exclusively at > 300 m depth, whereas *E. antarctica* is only known from South America and usually reported from < 300 m depth.

Our specimens compare favourably with samples described by Cairns (1983a), but differ in having the coenosteal pores distinguishable at the coenosteum surface, the presence of large pores at the surface, and having dactylostyles in the large dactylopores, never described before for this species. To date, the only other *Errina* species described with dactylostyles is *E. capensis* Hickson, 1912 from South Africa (Cairns and Zibrowius 2013).

Errina labrosa Pica, Cairns & Puce, sp. n.

http://zoobank.org/5F5BDBA9-ED95-47AC-8533-71208763C146

Figures 3–5

Holotype. BNHM 1977.8.10.2: four branches of a single colony, *Discovery* Expedition Sta 6, Tristan da Cunha, 3 miles N 30° E of Settlement, 80–140 m depth, 1 February1926 (in ethanol).

Paratypes. MNA 3085: two colonies, Cruise Icefish 2004 (dry); MNA 3087: several fragments (dry).

Diagnosis. The new species has a characteristic abcauline lip, ring palisade and one type of dactylopore with very elongated spines.

Description. The holotype (Figure 3a) is composed of several branches of a single colony. The larger branch is about 10 cm long and 9 cm wide. The other specimens

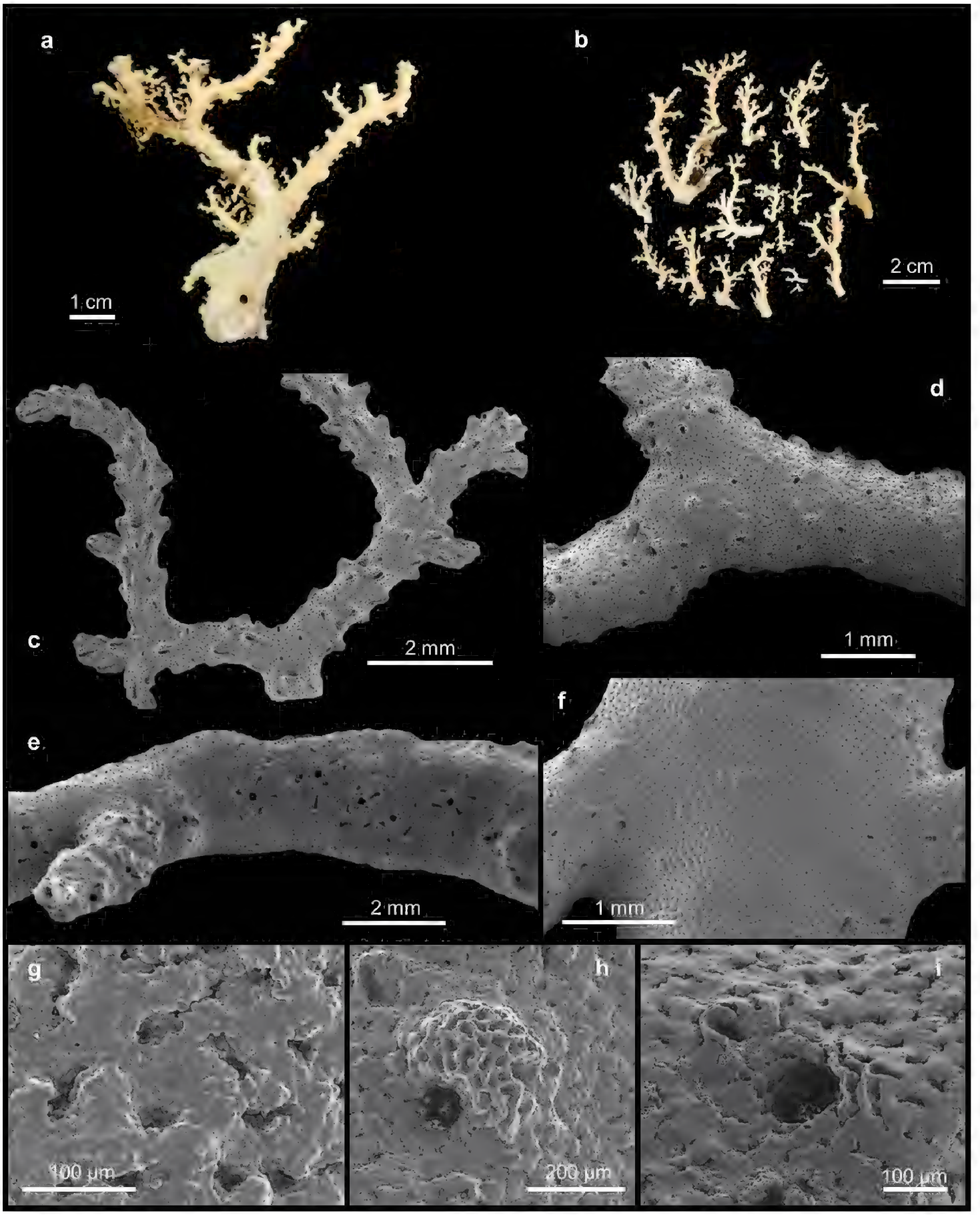

Figure 3. *Errina labrosa* sp. n. **a–b** Holotype. SEM micrographs of **c** spiny branch apex with gastropores and dactylopores uniformly distributed **d** middle portion of the colony **e** lateral view of the colony branch with gastropores are aligned and surrounded by the dactylopores **f** superficial coenosteum without pore **g** texture reticulate-granular **h** gastropore with lip **i** gastropore without lip.

(Figure 3b) consist of two large colonies and one small and broken colony attached to a black coral. All colonies have an wide base from where flabellate and uniplanar branches arise. Their bases are elliptical in cross-section and the axis of the largest colony is 6

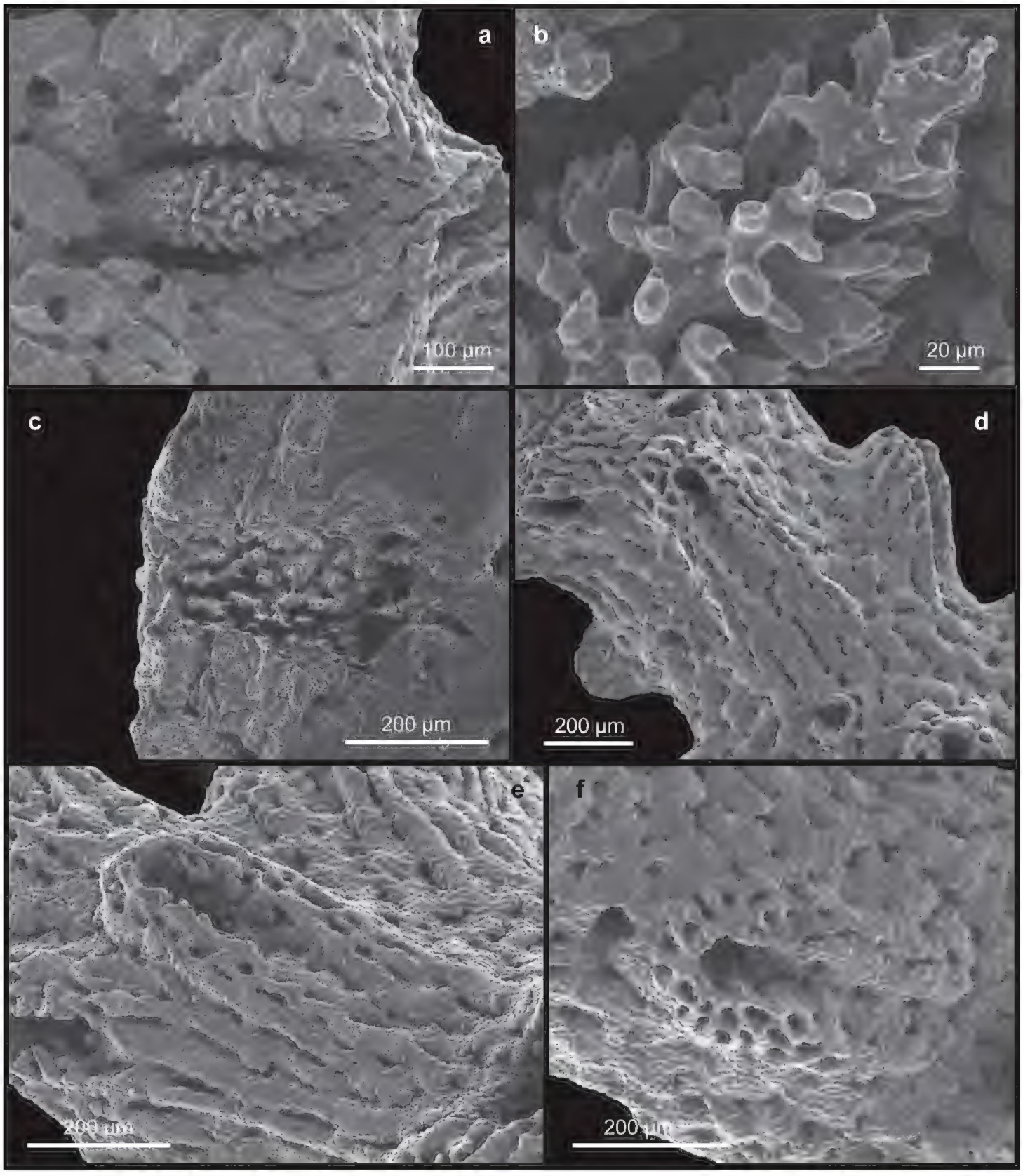

Figure 4. *Errina labrosa* sp. n. SEM micrographs of **a** gastrostyle **b** multitipped bifurcating spines of the gastrostyle **c** diffuse ring palisade **d–f** dactylopores from the apical region to the base.

by 4 mm. The apexes are up to 1 mm in diameter. The branches are irregularly sparse and unequal, without anastomosis.

The gastropores and the dactylopores are predominantly concentrated on the terminal branches (Figure 3c) and decrease in abundance towards the base (Figures 3d–f). In this region the pores remain confined to the lateral branch edges where the gastropores are aligned and surrounded by dactylopores characterised by a small spine.

The coenosteum is white-cream in colour and the texture is reticulate-granular with poorly-defined granules (Figure 3g). The strips are irregular in shape, 21–79 μm wide. The surface appears uniformly lumpy.

The gastropores are circular in shape (Figures 3h–i), 80–150 μm in diameter. Predominantly in the apical region of the colony they are bordered by a well-pronounced abcauline lip (Figure 3h). This lip is porous and rounded to rectangular in shape, up to 273 μm wide, and may bear one or two dactylopore spines. The gastropore tubes are cylindrical and shallow, gastrostyles are visible at the surface. The gastrostyle (Figure 4a) has a spindle shape, ornamented with multi-tipped bifurcating spines (Figure 4b) in the apical portion, while the basal region presents a small smooth constriction. They measure 205–289 × 68–114 μm (L:D=2.3–3.4). The wall of the gastropore tube bears a diffuse ring palisade (Figure 4c) composed of irregularly shaped elements up to 20 μm in diameter. Tabulae are absent.

Dactylopores are of one kind. In the apical branches they are adcauline and bordered by well-defined spines (Figures 4d–f; 5a). These spines are 104–244 μm long and 158–223 μm wide, truncate, with a long groove (the dactylotome) 300–550 μm long, which is oriented with an angle up to 45° with respect to the branch surface. Laterally, the spines show the same texture as the surface, while the internal wall is characterised by rudimentary dactylostyles, uniformly distributed on all surfaces (Figure 5b). The dactylostyle elements are rounded and 2–6 μm in diameter. The dactylotome is 48–73 μm wide. Proximally, the dactylopore spines are shorter with a smaller groove. In this region the spines are oriented in all directions and they are located mainly on the lateral side of the branches around the gastropores.

The ampullae (Figures 5c–d) are distributed homogenously over the colony. In the apical branches they are external while in the basal branches they are predominantly internal. The female ampullae, 550–842 μm in diameter, are round in shape but appear hemispherical from outside, and may have some dactylopores above them (Figure 5c) and an efferent pore on one side (Figure 5c). The male ampullae, 400–500 μm in diameter, are also round in shape (Figure 5d). No efferent pores were observed for them.

Remarks. Among the 25 known species of *Errina*, the only two other species having a gastropore lip, ring palisade and one type of dactylopore, as in our species, are *E. cheilopora* Cairns, 1983 and *E. reticulata* Cairns, 1991. The gastropore lip of these two species projects over the gastropore (Cairns 1991) and therefore differs in shape with respect to the lip observed in our specimens. In addition, both species have large gastropores (180–330 μm and 140–200 μm, respectively) and mainly show a linear-granular texture (Cairns 1991). Our specimens show a characteristic gastropore lip and very elongated dactylopore spines, which distinguish *E. labrosa* easily from the other species. Moreover, from a geographic point of view, *E. labrosa* together with *I. spinosa* (see above) represent the first identified stylasterids from the Tristan da Cunha Archipelago in the central part of the South Atlantic Ocean.

Errina was reported earlier from Tristan da Cunha by Moseley (1881) based on a specimen dredged by the *Challenger* Expedition (Sta. 135), which was identified as *E. labiata* (now *Inferiolabiata labiata*). Boschma (1964) doubted this identifica-

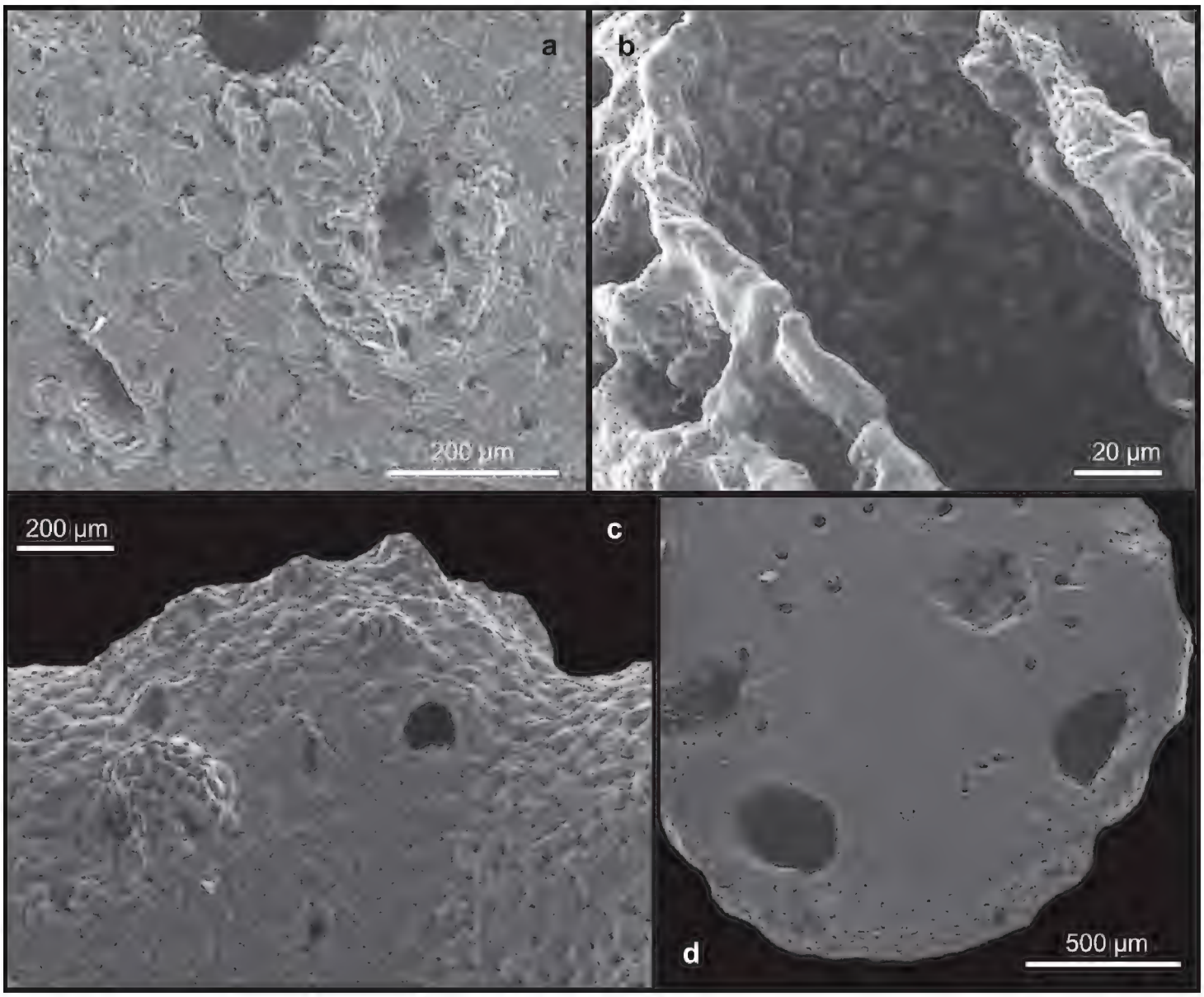

Figure 5. *Errina labrosa* sp. n. SEM micrographs of **a** dactylopore without spine **b** dactylostyle **c–d** ampullae.

tion because he noted that the openings of the groove spines of the dactylopores are turned toward the basal part of the colony instead of the apical part, as in *I. labiata*. He identified the specimen as *Errina gracilis*. Subsequently Cairns (1983a), reviewing the stylasterids from the Antarctic and Subantarctic region, reidentified the same specimen as *Errina* (*Errina*) sp. to because its poor description that did not allow a correct identification and therefore a comparison with our specimen is impossible.

Etymology. From the Latin word *labrum* (meaning lip) for the characteristic abcauline lip of the gastropores.

Scalpellid barnacles associated with stylasterid corals

The stylasterid *Errina fissurata* is reported as host for two different scalpellids (Table 1). One of them is *Trianguloscalpellum* sp. (Arcoscalpellinae, Figures 6a, b) on specimens MNA 3079 and 3082, while the other is *Ornatoscalpellum* cf. *vanhoeffeni* (Scalpellinae, Figure 6c) on specimen BNHM 1977.8.10.26. In all specimens the peduncles are par-

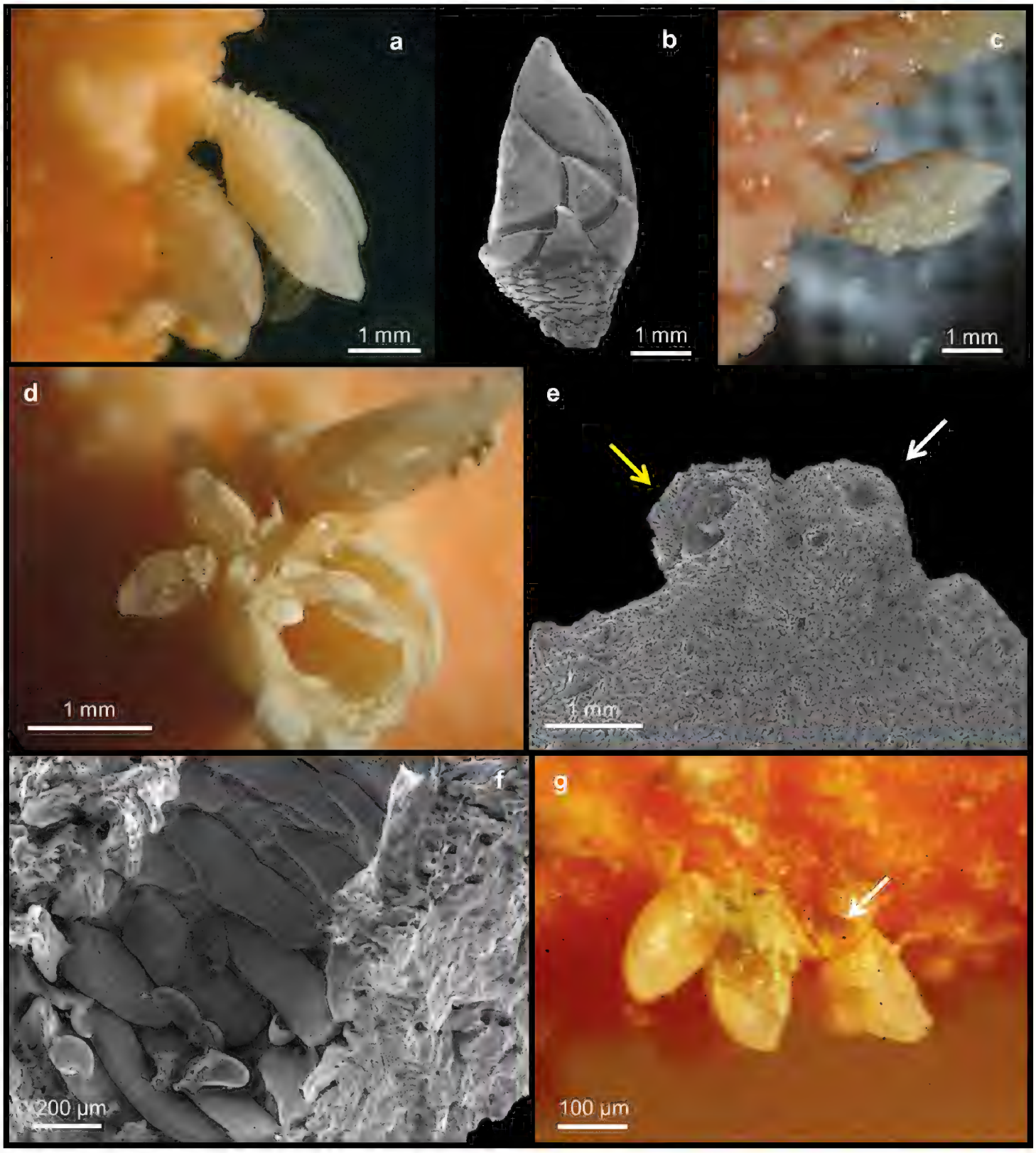

Figure 6. *Errina fissurata.* **a** Specimen with *Trianguloscalpellum* sp. **b** SEM of *Trianguloscalpellum* sp. **c** specimen with *Ornatoscalpellum* cf. *vanhoeffeni* **d** peduncular plates in cavity in coral coenosteum **e** SEM of where a barnacle was detached (yellow arrow) next to a superficial bump (white arrow) **f** peduncular scales in a bump **g** young barnacles one with peduncle in a dactylopore (arrow).

tially covered by a thin layer of coenosteum (Figures 6a, c). By removal of the unburied portion of the peduncle supporting the capitulum, a peduncular cavity within the peduncular plates can be seen penetrating deep into and surrounded by coral coenosteum (Figure 6d). Moreover, on the surface of *E. fissurata* corals several irregular calcareous bumps can be observed (Figure 6e), which are filled with peduncular scales (Figure 6f). At the base of one of these barnacles, several juvenile barnacles are found (Figure 6d). Similar young specimens have been found at some distance from mature ones attached

Table 1. Five stylasterid species and the eight scalpellids associated with them.

Stylasterid corals	Scalpellomorph barnacles
Stephanohelia sp. New Caledonia, 550 m	scalpellid sp. 3
Inferiolabiata spinosa Cairns, 1991 Tristan da Cunha, 80–140m	*Arcoscalpellum* sp. 2
Errina antarctica (Gray, 1872) Off Falkland Islands 79–370 m	scalpellid sp.1, scalpellid sp. 2 and *Ornatoscalpellum* cf. *gibberum*
Errina fissurata (Gray, 1872) off Daniell Peninsula, Antarctica, 438–610 m	*Trianguloscalpellum* sp. and *Ornatoscalpellum* cf. *vanhoeffeni*
Errina labrosa sp. n. Tristan da Chuna, 80–140 m	*Arcoscalpellum* sp. 1

to the surface or inside dactylopores of the host coral (Figure 6e). The barnacles on *E. fissurata* are scattered about mainly on the apical region of the corals.

The new species, *Errina labrosa* is observed in association with *Arcoscalpellum* sp. 1 (Figure 7a, b), while the species *Inferiolabiata spinosa* (Figure 7c) hosted *Arcoscalpellum* sp. 2 (Figure 7d) (Table 1). Specimens of these two cirripedes are attached to the surface of the corals albeit their peduncles are not covered by the coenosteum (Figures 7a–c). Moreover, when such occasional arcoscalpellines are detached nothing more than small depressions are left behind on the coral surface, and no recently settled juveniles were found around them. In *E. labrosa* individuals of *Arcoscalpellum* sp. 1 are scattered along the length of the colonies, while in *I. spinosa*, *Arcoscalpellum* sp. 2 is mainly distributed over the apical portions (Figure 7c).

Three different scalpellids are found in association with three different specimens of *Errina antarctica*: scalpellid sp.1 on specimens BNHM 1977.8.10.17, scalpellid sp.2 on BNHM 1977.8.10.20 (Figure 7e) and the scalpelline *Ornatoscalpellum* cf. *gibberum* on BNHM 1977.8.10.34 (Figure 7f) (Table 1). Individuals of scalpellid sp. 2 (Figure 7e) are concentrated in a mass on the basal portion of the stylasterid. While attached to the coenosteum, their peduncles are not covered by it. On the other hand, individuals of *O.* cf. *gibberum* are scattered individually over the entire length of the coral colony (Figure 7f). In this species too the peduncle remained uncovered by the coral coenosteum. The same can be said for scalpellid sp. 1, but in this case the coral surface several little bumps are present, circular in shape and with a small depression on the top (Figure 7g). No peduncular scales are visible in the depressions.

The stylasterid *Stephanohelia* sp. has been observed to host a single unidentified scalpellid, sp.3 (Figure 7h) (Table 1) which is located in the middle portion of the coral colony and has its peduncle covered by the coral skeleton up to the capitulum (Figure 7h). No other bumps or scars are observed on the coral surface.

In all cases the barnacles are attached through living tissue of the stylasterids, where their cyprid larvae had settled.

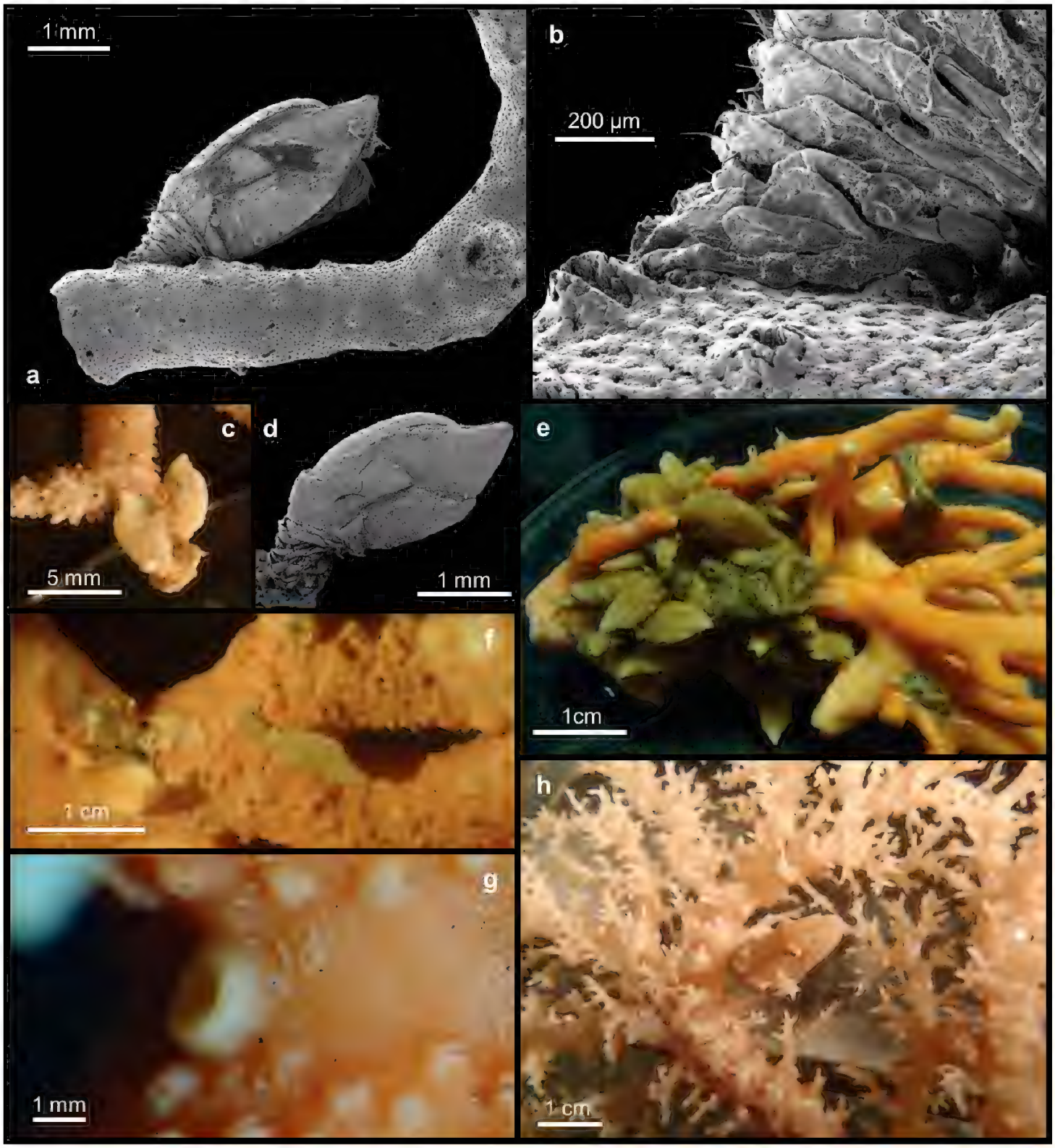

Figure 7. a–b Peduncle of *Arcoscalpellum* sp. 1 not covered by coenosteum of *Errina labrosa* sp. n. **c–d** Peduncle of *Arcoscalpellum* sp. 2 not covered by coenosteum in *Inferiolabiata spinosa* and SEM micrograph of same species **e** scalpelline sp. 2 concentrated in the basal portion in *Errina antarctica* **f** peduncle *Ornatoscalpellum* cf. *gibberum* attached to but free of coral skeleton in *Errina antarctica* **g** circular bumps with little depressions on the top in *Errina antarctica* **h** scalpelline sp. 3 with peduncle fully and lower margin of capitulum partially covered by the calcareous skeleton of *Stephanohelia* sp.

Discussion

The Stylasteridae of the South Atlantic Ocean, between the Antarctic and the Tropic of Capricorn, with a total of 22 known species, are poorly known (Boschma 1957, Cairns 1983a, Cairns and Zibrowius 2013). They are largely distributed along the

coasts of South America and South Africa, except for *Errina labiata* (see remarcks of *Errina labrosa* sp. n.) sampled from Tristan da Cunha during the *Challenger* Expedition (Moseley 1881). This identification was deemed highly questionable by both Boschma (1964) and Cairns (1983a) and currently it is just known as *Errina* sp. (Cairns 1983a). Thus, *E. labrosa* sp. n. and *Inferiolabiata spinosa* represent the only two identified stylasterid corals known from this locality. This Archipelago is considered part of the Temperate South America Region (Briggs 1974, Briggs and Bowen 2013), where 16 stylasterid species were reported from along the coasts of South America (Cairns 1983a).

Associations between cirripeds and cnidarians are fairly common in both shallow and deep water, involving numerous species of coral-associated barnacles. These include inconspicuous burrowing barnacles or acrothoracicans (Kolbasov 2009), which burrow in limestone and coral skeletons, and the conspicuous shallow-water balanomorph thoracicans of the family Pyrgomatidae (Simon-Blecher et al. 2007, Malay and Michonneau 2014), which settle on and keep pace with the growing coral skeleton (Ross and Newman 1973). Stalked barnacles have been recorded in association with some deep-water cnidarian taxa such as black corals (Molodtsova and Poltarukha 2008, Bo et al. 2012), gorgonians (Buhl-Mortensen and Mortensen 2004a, 2004b, 2005) and scleractinian corals (Newman et al. 2002). There is but one previous record of an association between stylasterid corals and a stalked barnacle (Newman and Ross 1971) even though several taxonomic papers provide information about symbionts of stylasterids (Zibrowius 1981, Goud and Hoeksema 2001, Puce et al. 2009, Pica et al. 2012). General works on stylasterids such, as Cairns (2011) and earlier, only mention barnacles in passing. That leaves Pica et al. (2012) for an overview, upon which the following list is based.

Subclass Cirripedia Burmeister, 1834 (those previously known associated with shallow as well as deep-water stylastrid corals, plus the scalpellids (Table 1))

Superorder Acrothoracica Gruvel, 1905

Order Lithoglyptida Kolbasov, Newman & Høeg, 2009

Family Lithoglyptidae Aurivillius, 1892

Armatoglyptes stirni (Turquier, 1987), off Strait of Gibraltar (Cape Spartel), in *Errina aspera* (L.) and other corals, 90–390 m (Kolbasov 2009).

Lithoglyptes s.l. in *Paraerrina decipiens* Brock, 1942 from Mauritius (Zibrowius 1981).

Order Cryptophialida Kolbasov, Newman & Høeg, 2009

Family Cryptophialidae Gerstaecker, 1866

Australophialus pecorus Turquier, 1985, off Strait of Gibraltar (Cape Spartel), in *Errina aspera* (L.) ~200 m and other corals between 20–390 m (Kolbasov 2009).

Australophialus tomlinsoni (Newman & Ross, 1971), off Ross Sea and Antarctic Peninsula, in skeletons of *Errina* sp. and other invertebrates, ~400 m (Newman and Ross 1971).

Superorder Thoracica Darwin, 1854

Order Scalpelliformes Buckeridge & Newman, 2006

Family Scalpellidae Pilsbry, 1907

Three species unidentified to genus herein, two on *Errina antarctica*, off Falkland Is. 79–370 m and one on *Stephanohelia* sp. New Caledonia 500 m.

Subfamily Scalpellinae Pilsbry, 1907

Ornatoscalpellum gibberum (Aurivillius, 1892), off Tierra del Fuego on *Errina* cf. *antarctica* (Gray, 1872), 250 m (Newman and Ross 1971).

Ornatoscalpellum cf. *gibberum* (Aurivillius, 1892) on *Errina antarctica* off Falkland Is, 79–370 m (Aurivillius 1892).

Ornatoscalpellum cf. *vanhoeffeni* (Gruvel, 1907) on *Errina fissurata* off Daniell Peninsula, Antarctica 438–610 m (Gruvel 1907).

Subfamily Arcoscalpellinae Zevina, 1978

Trianguloscalpellum sp., on *E. fissurata* (Gray, 1872) from off Daniell Peninsula, Antarctica 438–610 m (Gray 1872).

Arcoscalpellum sp. 1 and 2, one on *E. labrosa* sp. n., the other on *Inferiolabiata spinosa* Cairns, 1991, all from Tristan da Chuna, 80–140 m (Cairns 1991).

Order Sessilia Lamarck, 1818

Suborder Verrucomorpha Pilsbry, 1916

Family Verrucidae Darwin, 1854

Verruca s.l. on *Errina dabneyi* (De Pourtalès, 1871) from Açoc Seamount at 400 m (Braga-Henriques et al 2010, Braga-Henriques pers. comm.).

Suborder Balanomorpha Pilsbry, 1916

Family Pachylasmatidae Utinomi, 1968

Pachylasma giganteum (Philippi, 1836), Strait of Messina to off W. Africa, facultative with *Errina aspera* (L.), at shelf break, 150–200 m (Darwin 1854, Zibrowius 1981, Fredj and Giermann 1982, Di Geronimo and Fredj 1987, Zibrowius and Cairns 1992, Foster and Buckeridge 1995, Salvati et al. 2010).

Family Archaeobalanidae Newman & Ross, 1976

Solidobalanus enbergi (Pilsbry, 1921) shallow water, facultative on a stylasterid; possibly a senior synonym or sibling of *Armatobalanus nefrens* (see Young and Shimek 1982).

Armatobalanus nefrens (Zullo, 1963) shallow water, generally in *Stylaster californicus* (Verrill, 1866) and *Errinopora pourtalesi* (Dall, 1884).

Family Pyrgomatidae Gray, 1825

?*Pyrgoma* sp. on *Stylaster ramosus* Broch, 1947 from Tanzania, shallow water, possibly a pyrgomatid, but not likely a *Pyrgoma* species as presently known.

?*Pyrgoma* sp. on *Stylaster scabiosus* Broch, 1935 from Mauritius, shallow water, possibly a pyrgomatid, but not likely a *Pyrgoma* species as presently known.

Family Balanidae Leach, 1806

Balanus nubilus Darwin, 1854, intertidal and shallow water, occasionally all but overgrown by a *Stylaster* sp. in British Columbia.

Only two previously recorded cases of associations between scalpellomorphs and cnidarians provided with a hard calcareous skeleton are known, one illustration of

Ornatoscalpellum gibberum (Aurivillius, 1892) on *Errina* sp., likely *E. antarctica* (Newman and Ross 1971, Plate XIII), and the other of calanticids of the *Scillaelepas* complex on scleractinians from North Atlantic and New Zealand (Newman et al. 2002).

The scapellids reported here have been found in different positions on the stylasterid colonies and also in different stages of development. On the colony of *E. fissurata* and *E. antarctica* a morphological reaction to the presence of the symbiont has been observed. In fact, the cirriped induces or allows the production of a calcareous collaret surrounding the lower portion of its peduncle. A similar arrangement was reported by Newman et al. (2002) in the association between calanticid scalpellomorph and the scleractinian, *Lophelia pertusa*, where it settled in the coral calices. The presence of the barnacle caused coral skeleton or coenosteum to grow up around the base of the barnacle peduncle in much the same manner as seen here in some of the stylasterids. Regarding black corals, Bo et al. (2012) confirmed previous reports that the barnacle's settling induces a skeletal reaction resulting in an outgrowth of skeletal tissue with modified spines, and this can apparently also occur in cases involving some stylasterids-inhabiting barnacles (Figure 7h).

It was observed that when a cirriped accidentally detaches or dies, the hydroid partially plugs the gall with skeleton material which remains clearly visible as a bump-like scar. On the internal face of the bump the peduncular scales of the barnacle are still visible (Figures 6e, f). Similar attachment scars consisting of scleractinian skeleton material are reported by Newman et al. (2002, Figure 3 B and C) but here the cavity was only partially coated, not filled by the coral.

Several scalpellid individuals in different early stages of growth were found on colonies of *E. fissurata*. The cyprid larvae settled on the peduncle of established individuals as well as directly on the coral surface. In the latter case the cyprid larvae may settle inside dactylopore openings.

Conclusions

The study of the Stylasteridae corals from European museum collections did not only reveal various associations between stylasterid corals and pedunculate barnacles, but also allowed the description of *Errina labrosa* sp. n., which also participated in this association.

Overall, eight scalpellid species are recorded in association with five stylasterid coral species belonging to at least three genera. Our study suggests a lack of host specificity in this association. In fact, several barnacle species are found to be associated with *Errina fissurata* and *E. antarctica*, but it appears that in a single host coral colony only a single barnacle species can be represented. Although no specific association has been found, different grades of reaction to the symbiosis have been recorded in the coral. In *E. labrosa* and *I. spinosa* no reaction has been observed, while in *E. fissurata* and *Stephanohelia* sp. the coenosteum covered the peduncles of both observed barnacles species. *Errina antarctica* shows both kinds of interaction. This suggests that the reaction of stylasterid corals depends on the barnacle species, but because a wide range of sizes (ages)

of each species was not available, further investigations are needed to test this hypothesis. The symbiosis between stylasterid corals and scalpellid barnacles, albeit relatively rare, is largely confined to vulnerable marine ecosystems of the Southern Ocean (Jones and Lockhart 2011). Such biodiversity is not spread evenly across the ocean floor but follows complex patterns determined by climate, geology and evolutionary history.

Acknowledgements

We want to thank Dr. Stefano Schiaparelli (Museo Nazionale dell'Antartide Felice Ippolito, Genova), Dr. Andrew Cabrinovic (Natural History Museum, London), Dr. Bert W. Hoeksema (Naturalis Biodiversity Center, Leiden) and Dr. Aude Andouche (Muséum National d'Histoire Naturelle, Paris) for access to the coral collections. We thank the anonymous reviewers for their comments, which greatly improved this manuscript. This research received support to the first author for her visit to BNHM (London) and NBC (Leiden) from the SYNTHESYS Project http://www.synthesys.info/ financed by the European Community Research Infrastructure Action under the FP7 Integrating Activities Programme.

References

Aurivillius CWS (1892) Neue Cirripeden aus dem Atlantischen, Indischen und Stillen Ocean. Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar 3: 123–134.

Bo M, Lavorato A, Di Camillo CG, Poliseno A, Baquero A, Bavestrello G, Irei Y, Reimer JD (2012) Black coral assemblages from Machalilla National Park (Ecuador). Pacific Science 66: 63–81. doi: 10.2984/66.1.4

Boschma H (1957) List of the described species in the Order Stylasterina. Zoologische Verhandelingen, Leiden 33: 1–72.

Boschma H (1963) On the stylasterine genus *Errina*, with the description of a new species. Proceedings Koninklijke Nederlanse Akademie van Wetenschappen (C) 66: 331–344.

Boschma H (1964) *Errina* (*Lepidopora*) *decipiens*, a new stylasterine coral from the West Indies. Proceedings Koninklijke Nederlanse Akademie van Wetenschappen (C) 67: 55–63.

Boschma H (1966) Stylasterina. B.A.N.Z.A.R.E. Reports (B) 9: 109–120.

Boschma H, Lowe TP (1969) Distribution of selected groups of marine invertebrates in waters south of 35°S latitude, Stylasterina. Antarctic Map Folio Series 11: 14–15.

Braga-Henriques A, Carreiro-Silva M, Porteiro FM, de Matos V, Sampaio I, Ocaña O, Avila SP (2010) The association between a deep-sea gastropod *Pedicularia sicula* and its coral host *Errina dabneyi* in the Azores. ICES Journal of Marine Science 68: 399–407. doi: 10.1093/icesjms/fsq066

Briggs JC (1974) Marine zoogeography. McGraw-Hill, NewYork, 475 pp.

Briggs JC, Bowen BW (2013) Marine shelf habitat: biogeography and evolution. Journal of Biogeography 40: 1023–1035. doi: 10.1111/jbi.12082

Broch H (1935) Einige Stylasteriden (Hydrokorallen) der Ochotskischen und Japanischen See. Explorations des mers d' URSS 22: 58–60.

Broch H (1942) Investigations of Stylasteridae (Hydrocorals). Skrifterutgittav Norske Videnskaps-Akaddemi I Oslo. 1. Matematisk-Naturvidenskapelig Klasse 3: 1–113.

Broch H (1947) Stylasteridae (Hydrocorals) of the John Murray Expedition to the Indian Ocean. Scientific reports of the John Murray Expedition 26: 33–46.

Broch H (1951) Stylasteridae (Hydrocorals) from the Southern Seas. Discovery Report 26: 33–46.

Buhl-Mortensen L, Mortensen PB (2004a) *Gorgonophilus canadensis* n. gen., n. sp. (Copepoda: Lamippidae), a gall forming endoparasite in the octocoral *Paragorgia arborea* (L., 1758) from the Northwest Atlantic. Symbiosis 37:155–168.

Buhl-Mortensen L, Mortensen PB (2004b) Symbiosis in deep-water corals. Symbiosis 37: 33–61.

Buhl-Mortensen L, Mortensen PB (2005) Distribution and diversity of species associated with Deep-sea gorgonian corals off Atlantic Canada. In: Freiwald A, Roberts JM (Eds) Cold-water Corals and Ecosystems. Springer-Verlag, Berlin, Heidelberg, 849–879.

Cairns SD (1983a) Antarctic and Subantarctic Stylasterina (Coelenterata: Hydrozoa). Antarctic Research Series 38: 61–164. doi: 10.1029/AR038p0061

Cairns SD (1983b) A generic revision of the Stylasterina (Coelenterata: Hydrozoa). Part 1. description of the genera. Bulletin of Marine Science 33: 427–508.

Cairns SD (1991) The marine fauna of New Zealand, Stylasteridae (Cnidaria, Hydroida). New Zealand Oceanographic Institute Memoir 98: 1–179.

Cairns SD (2011) Global Diversity of the Stylasteridae (Cnidaria: Hydrozoa: Athecatae). PLoS ONE 6(7): e21670. doi: 10.1371/journal.pone.0021670

Cairns SD (2014) *Errina* Gray, 1835. In: Schuchert P (2014) World Hydrozoa database. Accessed through: World Register of Marine Species at http://www.marinespecies.org/aphia.php?p=taxdetails&id=117242

Cairns SD, Zibrowius H (2013) Stylasteridae (Cnidaria, Hydrozoa, Filifera) from South Africa. Zootaxa 3691(1): 001–057. doi: 10.11646/zootaxa.3691.1.1

Dall WH (1884) On some hydrocorallinae from Alaska and California. Proceedings of the Biological Society of Washington 2: 111–115.

Darwin C (1854) A Monograph on the Sub-Class Cirripedia. Ray Society, London.

Di Geronimo SI, Fredj G (1987) Lesfonds à *Errina aspera* et *Pachylasma giganteum*. In: Barrier P, Di Geronimo I, Montenat C (Eds) Le Détroit de Messine (Italie), évolution tectono-sédimentaire récente (Pliocéne et Quaternaire) et environnement actuel. Document et Travaux Institut Géologique Albert De Lapparent (IGAL) 11: 243–247.

Foster BA, Buckeridge JS (1995) Barnacles (Cirripedia: Thoracica) of seas off the Straits of Gibraltar. Bulletin du Museum National d'Histoire Naturelle. Section A: Zoologie Biologie et Ecologie Animales 17: 163–191.

Fredj G, Giermann G (1982) Observations en soucoupe plongeante SP 300 des peuplements d'*Errina aspera* (L.) (Stylasterina) du détroit de Messine. Téthys 10: 280–286.

Goud J, Hoeksema BW (2001) *Pedicularia vanderlandi* spec. nov., a symbiotic snail (Caenogastropoda: Ovulidae) on the hydrocoral *Distichopora vervoorti* Cairns and Hoeksema, 1998 (Hydrozoa: Stylasteridae), from Bali, Indonesia. Zoologische Verhandelingen, Leiden 334: 77–97.

Gray JE (1872) Notes on corals from the South and Antarctic Seas. Proceedings of the Zoological Society of London 1872: 744–747.

Gruvel A (1907) Crustacea: VI. Cirrhipèdes. In: Zoology and botany (Invertebrata, marine Algae, Musci). National Antarctic Expedition 1901–1904, III: 1–4.

Häussermann V, Försterra G (2007) Extraordinary abundance of hydrocorals (Cnidaria, Hydrozoa, Stylasteridae) in shallow water of the Patagonian fjord region. Polar Biology 30: 487–492. doi: 10.1007/s00300-006-0207-5

Hickson SJ (1912) On the hydrocoralline genus *Errina*. Proceedings of the Zoological Society of London 1912: 876–898.

Hoeksema BW, Van der Meij SET, Fransen CHJM (2012) The mushroom coral as a habitat. Journal of the Marine Biological Association of the United Kingdom 92: 647–663. doi: 10.1017/S0025315411001445

Jones CD, Lockhart SJ (2011) Detecting Vulnerable Marine Ecosystems in the Southern Ocean using research trawls and underwater imagery. Marine Policy 35: 732–736. doi: 10.1016/j.marpol.2011.02.004

Kolbasov GA (2009) Acrothoracica, burrowing crustaceans. KMK Scientific Press Ltd., Moscow, 452 pp. doi: 10.1651/10-3319.1

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Laurentius Salvius, Holmiae, ii, 824 pp.

Linnaeus C (1767) Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Holmiae 1(2): 533–1327.

Malay MCD, Michonneau F (2014) Phylogenetics and morphological evolution of coral-dwelling barnacles (Balanomorpha: Pyrgomatidae). Biological Journal of the Linnean Society, London 113: 162–179. doi:10.1111/bij.12315

Molodtsova T, Poltarukha O (2008) Cuticular spines of *Oxynaspis* spp. (Pedunculata: Cirripedia): An inheritance from antipatharian host. Abstract 4th Deepsea Coral Symposium. National Institute of Water & Atmospheric Research (NIWA), Wellington, 215.

Moseley HN (1879) On the structure of the Stylasteridae, a family of the hydroid stony corals. Philosophical Transactions of the Royal Society of London 169: 425–503. doi: 10.1098/rstl.1878.0014

Moseley HN (1881) Report on certain Hydroid, Alcyonarian and Madreporarian corals procured during the voyage of H.M.S. Challenger in the years 1873–1876. Part 1. on the Hydrocorallinae. Report On The Scientific Results Of The Voyage Of H.M.S. Challenger Zool 2: 1–101.

Newman WA, Ross A (1971) Antarctic Cirripedia. American Geophysical Union. Antarctic Research Series 14: 1–257.

Newman WA, Ross A, Buckeridge JS (2002) Deep-water scalpellomorph/coral symbiosis (Cirripedia, Pedunculata/Hexacorallia, Scleractinia) in the North Atlantic. Crustaceana 75: 517–525. doi: 10.1163/156854002760095561

Newman WA, Jumars PA, Ross A (1976) Diversity trends in coral-inhabiting barnacles (Cirripedia, Pyrgomatinae). Micronesica 12: 69–82.

Patton WK (1994) Distribution and ecology of animals associated with branching corals (*Acropora* spp.) from the Great Barrier Reef. Bulletin of Marine Science 55: 193–211.

Philippi RA (1836) Cirripedia, in Enumeratio Molluscorum Sicilae cum viventium in tellure tertiaria fossilium quae in itinere suo observati. Berolini, 1–267.

Pica D, Bertolino M, Calcinai B, Puce S, Bavestrello G (2012) Boring and cryptic sponges in stylasterids (Cnidaria: Hydrozoa). Italian Journal of Zoology 79: 266–272. doi: 10.1080/11250003.2011.632384

Pilsbry HA (1921) Barnacles of the San Juan Islands, Washington. Proceedings of the U.S. National Museum 59(2362): 111–115.

Pourtalés de LF (1871) Deep-sea corals. Illustrate Catalogue of the Museum of Comparative Zoology of Harvard College 4: 1–93.

Puce S, Tazioli S, Bavestrello G (2009) First evidence of a specific association between a stylasterid coral (Cnidaria: Hydrozoa: Stylasteridae) and a boring cyanobacterium. Coral Reefs 28: 177. doi: 10.1007/s00338-008-0411-6

Roberts J, Wheeler A, Freiwald A (2006) Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312: 543–547. doi: 10.1126/science.1119861

Ross A, Newman WA (1973) Revision of the coral-inhabiting barnacles (Cirripedia: Balanidae). Transactions of the San Diego Society of Natural History 17: 137–174.

Ross A, Newman WA (1995) A coral-eating barnacle, revisited (Cirripedia; Pyrgomatidae). Contributions to Zoology 653: 129–175.

Salvati E, Angiolillo M, Bo M, Bavestrello G, Giusti M, Cardinali A, Puce S, Spaggiari C, Greco S, Canese S (2010) The population of *Errina aspera* (Hydrozoa: Stylasteridae) of the Messina Strait (Mediterranean Sea). Journal of the Marine Biological Association of the United Kingdom 90: 1331–1336. doi:10.1017/S0025315410000950

Simon-Blecher N, Huchon D, Achituv Y (2007) Phylogeny of coral inhabiting barnacles (Cirripedia; Thoracica; Pyrgomatidae) based on 12S, 16S and 18S rDNA analysis. Molecular Phylogenetics and Evolution 44: 1333–1341. doi: 10.1016/j.ympev.2007.03.026

Stella JS, Pratchett MS, Hutchings PA, Jones GP (2011) Coral-associated invertebrates: diversity, ecology importance and vulnerability to disturbance. Oceanography and Marine Biology: An Annual Review 49: 43–104.

Stokes C (1847) Remarks on some corals obtained from great depths in the Antarctic Ocean, in a letter from Charles Stokes to Captain Sir James C. Ross. In: Ross JC. A voyage of discovery and research in the southern and Antarctic regions during the years 1839–43, London, vol. 1, Appendix IV, 334–338.

Turquier Y (1985) Cirripèdes acrothoraciques des côtes occidentales de la Méditerranée et de l'Afrique du nord. Bulletin de la Sociéte zoologique de France 110: 151–168.

Turquier Y (1987) Cirripèdes acrothoraciques des cotes occidentales de la Méditerranée et de l'Afrique du Nord III. Lithoglyptidae et Trypetesidae. Bulletin Du Muséum National d'Histoire Naturelle, Paris, 4a sér., 9, section A, 2: 391–408.

Verrill AE (1866) Synopsis of the polyps and corals of the North Pacific Exploring Expedition, under Commodore C. Ringgold and Capt. John Rodgers, U.S.N. from 1853 to 1856. Collected by Dr. Wm. Stimpson, Naturalist to the Expedition. With descriptions of some

additional species from the west coast of North America III. Madreporaria. Communications of the Essex Institute, Salem 5: 17–50, pls. 1–2.

Young CM, Shimek RL (1982) Natural history of a barnacle-hydrocoral association in the San Juan Islands, Washington. 63rd Annual Meeting of the Western Society of Naturalists. Abstracts. Southern California Ocean Studies Consortium, California State University, Long Beach, December 27–30, 58.

Zibrowius H (1981) Associations of Hydrocorallia Stylasterina with gall-inhabiting Copepoda Siphonostomatoidea from the south-west Pacific. Part 1. On the stylasterine hosts, including two new species. Bijdragen tot de Dierkunder Amsterdam 51: 268–286.

Zibrowius H, Cairns SD (1992) Revision of the northeast Atlantic and Mediterranean Stylasteridae (Cnidaria: Hydrozoa). Mémoires du Muséum National d'HistoireNaturelle 153: 1–136.

Zullo VA (1963) A review of the subgenus *Armatobalanus* Hoek (Cirripedia: Thoracica) with the description of a new species from the California coast. Annals and Magazine of Natural History Series 13: 587–594.